

## 10 • Evolution and diversity under bark

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A dying tree opens a wide variety of habitats for colonisation by insects. The basic anatomy of the tree remains: there are heartwood, sapwood, phloem, cambiums and bark. The various layers differentiate further by size, regimes of dryness and temperature, height above ground and in other ways. Underground the tree supplies rotting roots and rootlets and in the soil surface a litter of fallen branches and twigs; below ground, on its surface, and in the tree's standing or fallen hulk come patchy invasions and the fruit bodies of the major fungi.

Such a complex of habitats would be expected to have a rich fauna of insects and this is the case. The richness most peculiar to it, however, and that on which I will concentrate this account, is not the most obvious kind. Compared to certain other broadly defined habitats the dead-tree complex is not outstanding in its total muster of species. A more remarkable diversity lies in the host of genera, families and higher taxa, which, themselves tending to be few in species or even monotypic, are to be found only in this complex (e.g., Stubbs, 1972), or which, if found elsewhere, extend only into other kinds of decaying plant litter.

In trying to understand this 'phytonecrophily' and perhaps specific 'arbornecrophily' of so many of the odd and 'primitive' taxa of entomology, it is necessary to bring into view another peculiar and under-commented richness of the dead-tree arthropod fauna. Besides the many cases of deep phyletic *divergence*, illuminating common ancestry with outside groups, dead trees are rich in examples of functional *convergence*. Examples of such convergence will also provide ongoing threads in the theme of this essay and interweave with the problem of phylogeny. Four groups are outlined in the following paragraphs. Jointly they refer to certain similarities in *breeding structure*. Effects of breeding structure will form the essay's tentative thread of explanation.

1. Dead trees, and especially their habitats that lie immediately beneath the bark, are very productive of examples of *wing polymorphism* (list in Appendix, Tables 6.2 and 6.3). Such polymorphisms seem to be almost never of the type that is simply switched by alternative genotypes; they are switched instead by environmental cues to habitat change (personal observations; Taylor, 1975; Hood, 1940; Bournier, 1961). Hence they tend to index the occurrence of colonies that inbreed to multiply\* and then disperse. Convergent cases of paedogenesis, combined or not with thelytoky (*Platosciara*, *Micromalthus*, *Heteropeza*,

\**Ptinella errabunda* is at once polymorphic for wings and wholly thelytokous (Taylor, 1975). Similar exceptions from sexuality are known in Psocoptera (New, 1971a, b) and of course, within summer clones, are ubiquitous in aphids.

etc.), have rather similar significance and are an extension of this adaptive pattern. More trivially, convergences to phoresy and to caduence of wings in adults, both characteristic in the habitat, are linked to the same pattern.

2. The occurrence and probable origin in this habitat of about four of the six or so inventions of *male haploidy* by insects (Hymenoptera, Thysanoptera, *Micromalthus*, certain Scolytidae; excluded are iceryine coccids and Aleyrodidae) is likely also to reflect a structure of local breeding. The situation for male-haploid Acarina may well turn out to be similar, while certain parahaplo-diploid groups (in Sciaridae and Cecidomyiidae) may be arrested steps in a similar direction (see Borgia, 1978).

3. At least two of the origins of advanced insect *social life* (termites and ants)\* have their place in this type of habitat (Malyshev, 1969). Here again special breeding structure and/or male haploidy are implicated (Hamilton, 1972, 1974). Cases of subsocial life in the dead tree complex are legion and without doubt many still await discovery. One example which seems novel enough to deserve mention here, even though somewhat marginal to our habitat and concerning a non-insect, is that presented by a certain social group-hunting pseudoscorpion which Dr. L. A. O. Campos pointed out to me in Brazil. By cooperatively securing legs or antennae, bands of these pseudoscorpions are able to capture ants (their principal prey) many times their own size and far larger than would otherwise be possible. Although these atemnids are found most commonly under bark flakes of living *Eucalyptus* (where they waylay mainly *Atta*), I had also noticed similar bands in the habitat more typical for the group, that is, under the main slabs of bark of dead trees. Here ants of a similar size, e.g., *Camponotus*, were common. A seemingly very similar gregarious and myrmecophilous species was described by Turk (1953) from Argentina.

4. Finally, as a less basic convergence, although one which is no less striking, we may note the very numerous developments of certain types of *sex dimorphism*. Frequently the cases are connected with subsociality and reflect particular roles of the male (including as usual, with regard to offspring care itself, a frequent lightness or lack of role). In and around dead trees and recently evolved out of them are found a great number of the wingless, or dwarf, or outsize, or bizarrely-armed insect males that are known (Hamilton, in 1978).

Following the hint from these four groups of examples, that habitats of the dead-tree complex tend to force certain kinds of breeding structure, it will be argued that, besides calling forth specifically the convergences mentioned, such breeding structure is favourable to rapid evolution in a most general way: several interconnected reasons for this will be given. As to what may have actually been achieved by such postulated rapid evolution in dead trees, the strongest claim – and, as I judge from preliminary reactions from entomologists, the most difficult of acceptance – will be that many of the major insect groups have diverged there. More precisely this claim is that the phyletic divergences which now give systematists their separations at generic, family and ordinal levels were initiated with disproportionate frequency among insects living in dead trunks and branches. Such a claim seems to be almost new: so far as I know only one author in a very brief note has argued for a special importance of dead trees in insect evolution (Mamaev, 1971). A weaker and doubtless more acceptable version of the claim will be simply the same with the proposed crucial habitat complex widened to refer to vegetation detritus generally, not just

\*Patterns of both solitary and social aculeate wasps are also conceivably derivable from a biofacies of roughly bethylid type in rotten wood (Malyshev, 1969). In social bees wing polymorphism in a hypothetical ancestor of this type could have left an impress which is now reascent in the juvenoid-controlled caste differences between queen and worker (Campos *et al.*, 1975).

to the hulks of woody plants. This version is much less novel (e.g., Ghilarov, 1956; Southwood, 1973; Hinton, 1977); but even if the phenomenon is not more special than this it is still perhaps useful to look over a theory of Ghilarov's (or Mamaev's) type with the focus on breeding structure instead of on the more physical factors that have usually been emphasised.

### Breeding structure

The argument will refer primarily to the *cavernous* quality of the insect living spaces which dead trees offer. Besides this an important auxiliary factor will be the uneven and *scattered* distribution of dead trees. This second factor, however, is less peculiar to dead trees since living trees tend to show it as well. Moreover, its consequences for evolution are already appreciated.

Sewall Wright has long claimed that species are best able to make rapid evolutionary advance if their populations are divided into many small quasi-isolated demes. Obviously rotting trees tend to impose subdivision. Tree bodies are large enough and often die in a sufficiently piecemeal way to provide food for several generations: yet in the end each is eaten up and dispersal enforced. Returning to the cavernous quality already mentioned, dead-tree insects tend to live *in* dead trees and at least for those whose colonies can run several generations, without being forced to emerge, this affects the rigour of their isolation. Of course, in theory, colonies on the outside of live trees could perennate much longer still but in practice their isolation is much less certain; predators can make such insects fly or jump off and winds can mix them.

Support for Wright's thesis has come in recent years from demonstrations that evolutionary rates, as measured by morphology and chromosome rearrangements, can differ very markedly from group to group, and from recent surveys of such differences (Wilson *et al.*, 1975; Bush *et al.*, 1977) which strongly implicate an effect from breeding structures. This is seen to work partly on the lines of Wright's prediction and partly on the basis of a founder effect through local isolation which aids the spread of chromosome rearrangements in a process that amounts to a kind of sympatric speciation (Bush, 1975; Wilson *et al.*, 1975). In so far as such speciation goes on in dead trees it may multiply species numbers less than it would elsewhere since the new karyotype may be more apt to take over the whole habitat from the old (see below); but if karyotype and morphology change are correlated in insects as they are in mammals the process is still important from the present point of view and one of the remarkable convergences of dead-tree fauna — that to male haploidy (also see below) — seems to attest this.

Wright's plasticity through drift and Bush's 'instant speciation' by no means exhaust the evolutionary facilitations that can arise from local isolation. Some others are briefly indicated in the following summary:

1. Evolutionary change facilitated through drift plus recombination (Wright, 1932 and later papers).
2. Social evolution promoted through kinship. Local kinship groups are an inseparable concomitant of genetic drift (Hamilton, 1964, and refs. in E. O. Wilson, 1975).
3. Karyotype plasticity (Wright, 1940; A. C. Wilson *et al.*, 1975). Via male haploidy (Hamilton, 1974; Borgia, 1978) this synergises (2).
4. Subdivision resists wide-scale disaster from drive (Hamilton, 1967; Wright, 1969). This point connects closely with (1), (2) and (3) but emphasises deme extinction.
5. Interspecies reciprocation and symbiosis. The Trivers argument for individuals can be

extended to relations of multi-generation local stocks (Trivers, 1971; Hamilton, 1972; D. S. Wilson, 1976, and in prep.).

6. Polymorphism promoted by disruptive or alternating selection for sedentary breeders and dispersers (Hamilton & Taylor, unpublished). Such polymorphism has synergised (2) in ants and termites.

#### Diversity in dead trees

Compared to living oak trees (Southwood, 1961) dead oaks do not have an impressively long species list of insects (Larkin & Elbourn, 1964; Fager, 1968). Inclusion of Acarina would reduce but not eliminate this contrast. Extension of the survey to other tree species on the other hand would accentuate the difference: considering the fauna of a whole British wood, and still more for that of a tropical forest, the part associated with dead trees will prove far less species-diverse than that associated with live vegetation.

This relative poverty in species extends, of course, to other detritus habitats and the reason for it certainly has to do with the chemical and other special defenses of living green plants (Levin 1976; Swain, 1977; Gilbert, this symposium). It is well known that the stage of scolytid attack through the bark to the phloem is normally about the last where host specificity is at all marked. Subsequently arriving insects (perhaps no worse than most humans faced with debris of a tree) are poor botanists: in Britain, for example, they very roughly separate into degraders of conifers or of hard woods, but in general they tend to ignore species and go for convergently similar conditions of bark and wood and state of invasion by fungi. Thus faunal lists for dead tree overlap very widely (Elton, 1966).

If important evolutionary advance has an equal chance of occurring in all species (as is suggested by Mayr, 1963) the diversity of species on living plants would be expected to give these groups a great advantage with respect to initiating major new groups. Since direct phytophages and also parasitoids contribute disproportionately to the immense total species list of the Insecta, this should apply particularly to them. Yet it can be said with near certainty that the main forks of the tree of insect evolution have not occurred in phytophages or parasitoids. Even for the predominantly phytophagous groups Lepidoptera and Hemiptera there is plenty of room for doubt that the common ancestor was phytophagous (McKay, 1970). For the Coleoptera such an ancestor is hardly considered (Crowson, 1974). The scattered distribution of predation in generally phytophagous groups suggests that a transition from phytophagy to predation is fairly easy. It probably occurs most often via cannibalism in circumstances of severe competition (Fox, 1975). However, possible cases of transition to detritophagy or mycetophagy seem much less common. This topic will be reconsidered below. As one immediate example, the recently preferred phylogeny of the Thysanoptera which I used to view as providing the most probable case of a fairly important reversion from green plants to fungi (Stannard, 1968) has been thrown into doubt by Mound and O'Neil (1974): the group which they highlight (Merothripidae) raises a new possible image of the ancestral thysanopteran.

As might be expected the evidence for important reversions from parasitoidal existence is also weak. The most that can be claimed is that the ancestry of the aculeate Hymenoptera probably includes forms with at least ectoparasitoid habits (Malyshev, 1969). Even this reversion can be partly turned to advantage for the present thesis in that the distribution of primitivity in Hymenoptera suggests that it occurred among parasitoids, very possibly polymorphic for wings, living in dead trees, rather than in parasitoids whose hosts were in more aerial habitats (Malyshev, 1969; Brothers, 1975).

If reversions from phytophagy and parasitism are few and special, the weight of species numbers associated with living vegetation and the smallness of the numbers associated with detritus can largely be dismissed from our argument.

### Primitivity in dead trees

#### PARADOX

Much more than in species numbers and superficial diversity, a serious, almost paradoxical, difficulty concerning the role claimed for dead trees arises when we consider how it is proper to interpret the present day taxonomic distribution of 'primitivity'. Dead-tree insects are especially apt to be categorised as primitive by taxonomists (see Table 10.1). It has to be admitted that the most obvious interpretation of this is not at all that dead trees are the sites of radical innovations but rather that they are quiet backwaters serving as a kind of refuge for insect forms that have failed and vanished in the course of faster evolution going on elsewhere. The primitivity of dead-tree insects has indeed been referred to in such terms (e.g. Mamaev, 1975), and no doubt there are examples, particularly in those insects which have adapted to the difficult and nutritionally poor diets in the tree, to which the concept of a refuge and genetic stagnation really applies. But often the claims of systematists are confusing: they present the idea of a refuge and at the same time suggest that the habit of mycetophagy, for example, is more primitive in a group than that of feeding on the living parts of plants. This applies to Mamaev's discussion of Cecidomyiidae. The first impression on pulling slabs of bark from a dead tree trunk and seeing the dense and varied community, very rich in carnivores, that is present at a certain stage of decay of phloem is certainly not that of a quiet refuge (see also Beebe, 1923 Chapter 7). Yet, at the same time, to mention one group in particular, the beetle species in this subcortical community often present to the viewer a kind of synopsis of the whole classification of Coleoptera. Further, combining both the fossil and modern evidence on this group, Crowson (1974) has concluded that this is indeed the most probable habitat for the ancestral beetle.

Such a paradox may be partly resolved in the following way. Suppose a detritophagous stock evolves a phytophagous branch. Suppose that the lines diverge and attain, say, subfamily distinction, but all the time the phytophagous line speciates far more rapidly. A taxonomist trying to classify the whole group will have to heed and use far more characters in the phytophagous branch. The characters are needed to define numerous species and genera. Only a few characters will be needed in the detritophagous branch. Further, possibly it is just the characters that are most radical and pregnant with possibility of major evolutionary change which, in the few species of this detritophagous group, the taxonomist will neglect to emphasise because these characters are at once superfluous for definition and out of line with what are considered 'useful' kinds of character in the rest of his task. In other words, the primitivity of dead-tree insects could be partly an illusion arising out of the need to define species and create keys. For example, a horny quality of the adult forewings (e.g. *Issus*, *Merope*), or paedogenesis (e.g. *Heteropezini*), might be relatively overlooked as an apomorphic character of a dead-tree group because other characters had already sufficed to define it. Systematists have actually produced a name for such characters, autapomorphous, yet still seem to neglect them (Ashlock, 1976).

Consider *Platosciara perniciosus*. This is a parallel to *Heteropeza* in that, besides being a dead-tree insect in the wild (Steffan, 1975), it is also a pest of protected cultivation (Hussey *et al.*, 1969) and shows a kind of neoteny. Specifically, this species has a wingless and rather

worm-like morph (genuinely adult and represented in both sexes) as an alternative to the normal alate morph (Steffan, 1975). The place of the species in sciarine taxonomy is established, however, mainly on characters of the normal adult and Steffan's discovery and the strange form of the claustral adults is unlikely to affect this. If the alate form were abandoned due to success with another method of dispersal (e.g. endoparasitic like a *Deladenus* nematode, Bedding, 1967) the worm-like form could conceivably become the ancestor of a future 'order' of vermiform soil-dwelling insects, even with potentiality to become a new class.

#### DIRECTION OF TRANSITION: INTO OR OUT OF DEAD TREES?

The example of *P. pernicios* was chosen because the special evolutionary potential of neoteny is widely recognised, but, apart from this, the argument of the preceding section would apply equally well if the hypothesised original stock had been non-detritophage. In general whether a stock has emerged from dead trees (or simply from detritus) or has gone into it has to be settled from the particular evidence of the case including the hints as to adaptation that appear in the systematist's reconstruction of the original type of a group.

Thus the fact that, so far as I know, the only place where *Heteropeza pygmaea* can be reliably found in the wild is under dead bark, where, in Britain, it is an abundant and characteristic pioneer in the decay of phloem, strongly suggests that occurrence of this species in mushroom houses (Hussey *et al.*, 1969) is secondary. The case of *P. pernicios* is actually less certain because although known from rotting logs (Steffan, 1975) I do not know that this habitat is most typical in its native land, wherever this may be. Similarly, another sciarine, *Bradysia paupera*, may give a good illustration of a tentative switch of oviposition and larval feeding out of the usual habitat and on to green leaves (Hussey *et al.*, 1969); but this is more likely to be a switch out of soil than out of dead trees. Nevertheless, dead trees are indeed rich in sciarine genera (Tuomikoski, 1957). A more direct transfer to phytophagy from a subcortical habitat is likely in the mite *Rhizoglyphus echinopus* (Fager, 1968; Obreen, 1967), and such transfer is virtually certain in the case of the bug *Aradus cinnamomeus* (Usinger & Matsuda, 1959; Turček, 1964). At generic or higher levels Crowson (1974) instances other cases in Coleoptera.

Brief mention in this text of three other examples of probable emergence from dead trees must suffice.

Firstly, consider the beetle family Rhipiphoridae; this may be treated as a possible model for the unknown history of the parasitic order Strepsiptera. Females of the parasitic genus *Metoeus* rather unexpectedly lay their eggs on dead wood, although the larvae are parasitic on *Vespula*. Other rhipiphorids have larvae which are free-living in dead trees (Imms *et al.*, 1957). So this one family spans the life styles of a normal beetle and a stylops, and the oviposition site mentioned suggests dead trees as the likely ancestral habitat. Secondly, consider the path to another type of parasitism, that of Cimicidae. *Cimex* is flattened and also wingless and we would expect some sign of these characters in a bug proposed as its closest non-parasitic relative. Flattening suggests a subcortical insect and sure enough both characters are to be found under bark in representatives of the predatory and wing polymorphic genus *Xylocoris*. Usinger (1966) finds *Xylocoris* to be the anthocorid genus with certain characters most suggestive of a primitive cimicid. Here flattening and winglessness suggest the direction of evolution. The genus *Anthocoris* itself suggests a bridge from subcortical life to phytophagy: in summer *Anthocoris* species are important predators



Table 10.1. Primitivity in insects connected with dead trees

INSECT GROUP ORDER SUBORDER	In dead or dying trees		Primitive with respect to:	On or in live land plants (examples not mentioned)	Comments
	Dead tree association exists in:				
<i>Subclass</i> APTERYGOTA					
<i>Class</i> Collembola					
<i>Order</i> Arthropodea			Arthropodea	None	c.f. <i>Rhyniella</i>
<i>Order</i> Symphypleona	<i>Neumira</i> , etc			Some	
<i>Order</i> Protura	<i>Atlacma</i> , etc				
<i>Order</i> Diplura	Some		Insecta	None	
<i>Order</i> Archaeognatha	Some				
<i>Order</i> Thysanura	Some				
<i>Subclass</i> PTERYGOTA					
<i>Division</i> Palaeoptera: 2 orders and 5 suborders, all aquatic unconnected with terrestrial plants.					
<i>Division</i> Neoptera					
<i>Section</i> Polyneoptera					
<i>Order</i> Dictyoptera					
<i>Order</i> Blattaria	Many		Dietyo-Isoptera	Some	Note <i>Cryptocercus</i>
<i>Order</i> Mantodea	A few		Neoptera	Most	
<i>Order</i> Isoptera	Most		Neoptera	None	Primitive termites in wood
<i>Order</i> Zoraptera	All		Neoptera	None	Aquatic
<i>Order</i> Plecoptera	Some Archipteraria?		Plecoptera	None	Montane
<i>Order</i> Grylloblattodea	None?		Neoptera	None	
<i>Order</i> Phasmida	<i>Eurytanthia</i> , etc		Phasmida	Almost all	
<i>Order</i> Orthoptera					
<i>Order</i> Ensifera	<i>Detritivida</i> , etc		Ensifera	Most	
<i>Order</i> Coleltera	None?			Most	
<i>Order</i> Embioptera	Some		Neoptera	Some (bark)	Soil and litter typical
<i>Order</i> Dermaptera	Many		Neoptera	A few	Note flattened subcortical Apachyoidea
<i>Section</i> Paramacoptera					
<i>Order</i> Psocoptera					
<i>Order</i> Trogiomorpha	<i>Lepidotus</i> , etc		Psocoptera	?	Principally
<i>Order</i> Troctomorpha	<i>Embiolopsocinus</i> , etc		Psocoptera	None?	under or on bark
<i>Order</i> Eupsoecida	None?			Most	

Thysanoptera				
Terebrantia	Microthripidae		Terebrantia	Most
Tubulifera	Many			Many
Hemiptera				
Coleorrhyncha	None?		Hemiptera	All?
Homoptera	Some Fulgoroidea		Homoptera	Most
Heteroptera	Dipsocoromorpha		Heteroptera	Most
<i>Section</i> Oligoneoptera				Note also <i>Neostreptia</i> , <i>Orithetia</i> (see text)
Neuroptera				
Megaloptera	Raphidioidea, <i>Chaulioides</i>		Neuroptera	None
Planipennia	**			Most
Mecoptera				
Protomecoptera	Unknown		Mecoptera	?
Fumecoptera	None		Oligoneoptera	Many
Trichoptera	Xiphocentron		(not primitive)	None
Lepidoptera*	None?		Lepidoptera	All?
Zeugloptera	Some Hepialidae, etc		Monotrysa	Most
Monotrysa	Various			Most
Diptera				
Nematocera	Some, in about 1/2 of families		Diptera	Some
Brachycera	Some, in majority of families			Some
Cyclorhaphia	Some			Some
Hymenoptera				
Symphyta	Siricoidea, Orussoidea		Hymenoptera	Most
Apocrita	Various		Apocrita	Many
Coleoptera				
Archostemata	Cupesidae		Coleoptera	None
Adephaga	Rhyssodidae		Coleoptera	Some
Polyphaga	Many, in almost all families			Many

Table 10.1 shows a conservative classification of insects to the level of Sub-orders (or Orders, if Sub-orders are not defined), but with all wholly epizootic groups excluded. Column two indicates the degree of association of species with dead trees, and column three the extent to which these species are regarded as 'primitive' with respect to their own suborder or to some more inclusive taxon (a dash indicates that primitivity is indecisive). Column four indicates the extent of attachment of each group to living plants: no attempt is made to mention specific groups and status within these, since this would greatly lengthen and complicate the table to reveal only a minor extent of primitivity.

\*The earliest known Lepidopteran fossil is a larval head capsule in Cretaceous Amber embedded with webbing, frass and crumpled plant remains: this suggests a feeding site on or under bark or else in litter at ground level (McKay, 1970).

\*\*Larvae of Psychopidae and Berothidae under bark flakes — only on live trees? *Megathione* (Ichonidae)?

\*\*\*Species from living plants are mostly parasitoids of plant feeders; some are seed chalcids, gall wasps, etc.



of aphids, and feeding on the body fluids of aphids cannot be very different from imbibing phloem sap directly.

I do not know of any actually phytophagous Anthocoridae, but perhaps a parallel transition can be identified – my third example – in the Coccinellidae, where, along with the aphid-feeders, plant-feeding species also occur. Here, the divergence is more advanced and family Endomychidae is the proposed parallel to genus *Xylocoris* (although whether larval endomychids are predatory or mycetophagous I have not ascertained). Coccinellids have evolved preference for drier and quieter hibernacula than the sites under bark where one finds *Endomychus*; on the other hand *Anthocoris nemorum* can be found in winter under bark mixed with *Xylocoris* colonies and at such times is conceivably predatory there – in what is here suggested to be its ancestral home.

Examples of insects that have most probably entered dead trees from elsewhere appear to me much harder to find. This may be partly due to my current bias and I will be glad to be informed of counter-cases overlooked. Perhaps the best case noted so far is that of the genus *Forcipomyia*. Larvae of this genus are common under dead bark in Britain. They possess a closed tracheal system normally characteristic of aquatic larvae and in fact many related genera of the same family of flies (Ceratopogonidae) are aquatic as larvae (Saunders, 1924). It could be that the closed tracheal system was evolved for survival in species dwelling in bark habitats subject to frequent flooding and then later proved pre-adaptive for permanent life in water; but the opposite course of evolution seems at least equally likely. Outside the Insecta a rather similar example is provided by woodlice. These are isopod crustacea (Oniscoidea) and the majority of isopods are aquatic. On land some woodlice are, as the British common name implies, abundant under loose bark, but all are found widely in litter, compost and similar habitats as well. In Britain *Oniscus asellus* is, perhaps the most constant bark species and its slightly flattened form, so similar to that of some subcortical roaches, suggests bark as its ecological 'headquarters' (*sensu* Elton). It seems most likely that the ancestor of terrestrial Oniscoidea came ashore (probably in at least two invasions, Vandel, 1943) via litter and soil, as some isopods and amphipods and other primarily aquatic crustacean groups seem to be doing at the present day. However, isopods in *Limnoria* and *Chebur* suggest that a course from water directly into dead trees is at least possible.

Rather as woodlice seem recently to have gate-crashed the land fauna and, in consequence of a lack of groups adapted to exploit them, may obtain a kind of freedom of diverse habitats into which they can begin to radiate, so some *Drosophila* colonists which had the fortune to enter the Hawaiian Islands may have found a similar freedom, in this case probably mainly freedom from competitors. Superabundant speciation in the *Drosophila* in question gives their case a different complexion from the isopods, but the parallel to be pointed out here is that the colonist *Drosophila* stocks seem to have been particularly successful in invading the subcortical habitat (Carson & Kaneshiro, 1976). But again, an alternative possibility, that the invasion took place through species arriving in driftwood, should be borne in mind.

There are various enigmatic cases in Hemiptera which might be transferrals from phytophagy to mycetophagy. Most of them concern soil (Kuhnelt, 1961), but some refer to rotting logs, for example most of the Achilidae, or to rotting tree ferns, for example *Oliarus* in Cixiidae (Zimmerman, 1948). I do not know about the primitivity status of these log- and soil-associated groups within Fulgoroidea but this group itself is treated by Goodchild (1966) and other as the basal branch of Heteroptera. With Sternorrhyncha also the most primitive groups tend to be those most associated with soil and claustral habitats. Such a distribution of primitivity makes the mycetophagy which is, for example, at least sometimes indulged by *Orthezia* (Thorpe, 1968), lose weight as a counter-example. (A like argument

also applies to what may be reversion to mycetophagy in scarabaeids — Bornemissza, 1971; Howden, 1955).

A more serious implication in Hemiptera comes from the Peloridiidae, usually considered the basal branch for the whole order. If the common ancestor which this family has with the rest did indeed such mesophyll, as peloridiids are thought to do, then, in Goodchild's phylogeny, there is an important reversion in passing from this ancestor to the supposed litter-dwelling non-phytophagous ancestor of the Heteroptera. The change in the articulation of the rostrum to the front of the head is certainly suggestive of a move under bark. Predatory enicocephalids and anthocorids make good use of forwardly-directable mouthparts in this situation; yet achilids and mycetophagous thrips manage without them. The uncertain reversion indicated by peloridiids and also the general implication of their moss habitat will be touched on again below.

Rotten wood is favoured by very diverse groups as a site for hibernation (Elton, 1966) but transition into rotting wood in this sense is usually a trivial event from the point of view of breeding structure. Whether it carries an implication of 'ancestral familiarity' with dead wood is an intriguing question in view of the use of this site by *Anthocoris*, coccinellids, ichneumonids, etc (Larkin & Elbourn, 1964). Perhaps an equal list of cases with no such likely ancestral connection could be cited. *Vespa crabro*, a 'primitive' social vespine, uses dead wood for hibernation site, nest site and nest material; on the other hand *Vespula* queens seem to use equally readily any other hibernation site that offers suitable cover and microclimate. The same applies to *Bombus*. As regards wood-nesting in *Xylocopa*, Hurd (1958) claims that soil is the likely ancestral nest site, and Barrows (1973) equally claims this for log-nesting Halictinae. Wood or soil should make little differences to breeding structure in these very free-flying flower-visiting insects.

Some other cases of transition which might repay study are indicated in Table 10.1 and in the following additional list: Sminthuridae (Collembola); Liposcelidae (Psocoptera); Derbidae (Hemiptera); Chrysomeloidea, Scarabaeoidea (e.g. *Oryctes rhinoceros*), Curculionoidea, Scolytidae (e.g. *Hypothenemus*), Elateridae, Nitidulidae (Coleoptera); Hepialidae (Lepidoptera); Tipulidae, Lonchopteridae, Syrphidae, Phoridae (e.g. *Megaselia*), Dolichopodidae (Diptera). Possible trends in Scolytidae have already been outlined by Schedl (1958).

#### THE FOSSIL RECORD AND COMPARATIVE EVIDENCE

The record of arborescent land plants extends back as far as the record of insects but evidence directly connecting the two in the Palaeozoic is extremely scanty (Scott, 1977). This applies almost as much to evidence of attack on living plants, arborescent or not, where damage that could be attributable to insects should be relatively easy to recognise, as it does to evidence of inroads on dying and dead remains. As regards indirect evidence, the point can at once be made that the earliest of all known insects (using a broad view of the class), the collembolan *Rhyniella*, is remarkably like *Neanura muscorum* (Massoud, 1976), a species which occurs today under dead bark and in rotting wood. It is also to be noted that some forms of attack on tree detritus, especially the habit of feeding on the associated fungi, would leave little trace of any kind that could be fossilised, and that wet conditions such as prevailed where Palaeozoic plant fossils were formed are hostile even to the preservation of arthropod coprolites.

Standing dead lepidodendroid trunks of Carboniferous age on Arran, described by Williamson (1880) — hollow, and containing lodged within them twigs and 'leaves' and other

fragments of various plants (and all finally buried in volcanic ash) – represent not only the type of habitat where one would confidently search for *Neamura* today, but also just that kind of food object, discrete, bulky yet cavernous, which our hypothesis has required. These trunks hint that we need not take too seriously the lack of evidence of bored insect galleries in pre-permian plant remains. In truth such evidence of boring in the Palaeozoic seems to be scanty and unconvincing: sinuous engravings on the cortex of *Sigillaria* in Germany (Geinitz, 1885) look to me as attributable to, say, impressions left by fungal rhizophores as to galleries of insects; and, in some other fragments, holes indubitably bored by some animal are of a size too minute to be probable work of insects (Williamson, 1880).

Borings, however, appear in fossil wood of the Permian and so does bark (Crowson, 1974). As Hinton (1948) has noted, there is a basic conflict between burrowing and the possession of wings and the most striking solution of this has been holometabolous development. Perhaps a move by arborescent plants to protect phloem beneath bark (Smart & Hughes, 1973) was the principal stimulus to holometaboly. In this essay we are mainly concerned with the bonanza of *dead* phloem but no doubt in all ages there have been saprophagous insects that pressed their attacks earlier or brought in parasitic fungi to prepare ground ahead, much as cerambycids, scolytids and siricids do today; bark needs to protect against these too. In this connection it is interesting to note the somewhat unexpected appearance of ovipositors in certain Palaeozoic groups (Carpenter, 1977). Among their many other uses ovipositors serve to put eggs in deep crevices and under bark: ovipositors occur, for example, in various stages of evolution, in many present-day insects whose larvae live under bark or in wood (*Helops* and *Lonchaea* show cases of incipience). Species that lay eggs from the outside of bark are usually outbreeders, and this according to our thesis counter-indicates the ancient groups with such appendages as being quite perfect images of the ancestors of major groups of the present day; correspondingly, of course, a connection of ovipositors with apparent evolutionary stagnation (as in raphidians, cupedids, siricids, orussids) is not surprising. Adults going in under bark, going in further through flattening or by development of horny forewings (as in roaches, beetles, and some psocoptera – and perhaps also in *Issus*, *Merope* and others) or by dealation (as in some Embioptera, Isoptera, Zoraptera, Psocoptera, Thysanoptera and Hymenoptera), going perhaps further still through an apterous adult morph or total wing-loss (Appendix I, *Cryptocercus*, etc.), sending on unencumbered larvae ahead as specialised burrowers, finally as the ultimate development in a few lines, allowing those larvae to breed for themselves without any need for more space (*Heteropeza*, *Micromalthus*) – this whole sketched evolutionary sequence for the increasingly rapid penetration and utilisation of dead phloem hidden beneath bark seems to me eminently possible. One step is perhaps currently reillustrated by the sluggish 'pupal' stage of subcortical tubuliferan thrips. In the main stock formation of the pupa produced the great insectan advance to holometaboly.

#### BAST AND WOOD

Bast – that is, phloem plus cambiums – offers a rich and well-balanced diet. On the death of a tree these layers are the most speedily consumed. Sapwood is consumed more slowly and by fewer species. Lignified heartwood and suberised bark, where these are present, go more slowly still.

The wide variety of taxa that can be found directly under the bark has already been emphasised, and the same habitat has had repeated mention in connection with other phenomena. Besides consumers of dead plant tissues there are many species that feed

primarily on the bacteria, yeasts and fungi that are soon abundantly present, including on parts of those fungi that are primarily concerned with the decay of wood. There is also a surprisingly high diversity of predators. All these insects tend to be small, with a size range overlapping (e.g. *Ptinella*, 0.6 mm) that of typical Acarina, which group is itself abundantly and diversely represented. They also tend to have short generation times which, more than offsetting rather low total fecundities, gives them potential for high rates of increase. As our hypothesis requires, many species do indeed readily mate within the habitat and the inbreeding which this implies is reflected in biased sex ratios which further improve the potential for colonisation and increase. Polymorphism in colonial species of this habitat is summarised in Appendix 1. It might be thought that winglessness in a morph would always be a further device for greater effective fecundity and increase, as it is in all other winged/wingless morph comparisons that have ever been made in non-social insects. No doubt this is often the case with the subcortical polymorphisms but one notable exception has recently appeared.

Studying the very marked polymorphism found in both bisexual *Ptinella aptera* and thelytokous *P. errabunda*, Taylor (1975) found that winged females were longer lived, were more fecund and had larger spermathecas than their wingless counterparts. This is suggestive of the beginning of a termite-like social development. In fact on the basis of this example plus the general absence of wing polymorphisms in xylophagous insects, it can be suggested (Hamilton and Taylor, unpublished) that social termites arose from their roach-like ancestors in the habitat of dead phloem, and that *Cryptocercus* is consequently connected to them as a parallel invasion of the wood, rather than as a 'wax-work' image of their ancient way of life as is often implied (e.g. Wilson, 1971).

In contrast to the subcortical insects, those of dead wood are usually larger (and include the largest of all, e.g. *Titanus giganteus*, up to 200 mm), and tend to develop much more slowly; generation time of 2 or 3 years is common in temperate latitudes. Consequently wood feeders are rather slow to increase in a habitat and for reasons perhaps connected with this but not fully understood they are also much less inclined to endogamy and to claustral continuance of the colony even if the wood provides bulk for it (primitive termites, *Micromalthus* and perhaps passalids are exceptions here). As expected if mating is outside the log, sex ratios are on the whole normal; both parthenogenesis and wing polymorphism are almost unknown (termites and *Micromalthus* again excepted).

Bearing in mind reduced faunal competition and slower generation turnover and bearing in mind also the more outbred breeding structure, it is particularly here that we would expect to find true relict insects. And possibly the concept can apply, for example, to *Cryptocercus*, Cupesidae and Siricidae.

At the same time the wood has many obviously advanced invaders, for example Cerambycidae. These are suspected to have moved inward from the phloem relatively recently. Some lines in Scolytidae appear to be so evolving at the present time (Schedl, 1958). Where beetles move in as 'ambrosia' feeders the diet remains rich and rapid endogamous breeding is sometimes retained. Here might be mentioned the large genus *Xyleborus* which also illustrates various cases of transition towards attack on the green parts of living plants. *Micromalthus*, combining arrhenotoky, thelytoky and paedogenesis, is much less successful but confined within rotten wood its trend is similar but more extreme. Certain cecidomyiids, moving in through shrinkage cracks without ambrosia but again feeding on fungi and not on wood, offer rough parallels to the ambrosia beetles — *Pezomyia* (or, probably better, the little known *Micropteromyia*) parallel to *Xyleborus*, and *Heteropeza* parallel to *Micromalthus*.

### Primitivity in other habitats

Apart from habitats of the dead-tree complex, others especially frequently mentioned in connection with 'primitivity' are litter and soil, moss (and to some extent other primitive green plants), and finally fresh water. The living parts of higher plants tend to carry insects that taxonomists rate as relatively advanced, the main exception to this being, perhaps, an undue frequency of 'primitive' insects feeding on pollen and the pollen-producing organs of plants (see below). Seed insects, on the contrary, and also those of 'stored-product' type environments tend to be classed as advanced and so do parasites (probable routes to these various life-styles can be drawn out of dead trees via the hollows in which birds, lizards and mammals nest and keep their stores – for species suggestive of this see lists in Hicks, 1959).

Dung and carrion tend to carry types of rather intermediate primitivity. Carrion of large animals might at first thought seem very like the rich phloem masses of dead trees in size and nutritive value. Perhaps it is partly the quality of thinness that tends to reserve dead phloem for insects. Besides this carrion is even more scattered, even more nutritive, and less resistant to entry and destruction. Thus larger animals take a far larger share and tend to leave only dispersed fragments and bones – the latter a worse resource for insects even than the heartwood of trees. Altogether the attributes of carrion left available to insects almost necessitate that those that breed in it be good fliers and fly in every generation. This encourages panmixia. Excepting perhaps dried carcasses, carrion is too ephemeral to support colonies.

### MOSS

Plant litter and soil are habitats with no sharp separation from rotting tree trunks and branches. Moss too is intimately associated with all these, and like them provides sheltered and hidden spaces. The spaces in dense moss cushions may, like cavities in soil and wood (and like the similar spaces in dense grass tussocks), tend to encourage local inbred colonies. Yet, I believe – admittedly on no easily presented evidence – that feeding in living moss is more often derived from mycetophagy and detritophagy than vice versa. One example, that of *Peloriidae* again, must serve to illustrate both moss primitivity and this bias of the writer. The family was largely lost as an illustration of my dead-tree theme when I read that some members had been shown to exist in *Sphagnum* and other mosses distant from trees (Evans, 1941); however, this has not been shown for all species and I preserve a small hope that at least *Peloriidum hammoniorum* may prove mycetophagous in rotting wood: this species was first found under a rotten log, and it is perhaps significant that this is also the one species known to show wing polymorphism (China, 1962).

### LITTER AND SOIL

Almost every group mentioned in connection with dead trees in Table 10.1 also has representatives in other kinds of plant litter and in soil. Soil and litter insects likewise tend to be more 'primitive' than collateral groups that feed (not necessarily as herbivores) on aerial parts of living plants. The special case made for dead trees is based partly on the *a priori* considerations already mentioned and partly on an impression that evolutionary novelty is really more common in dead-tree insects than in those of soil. What has soil to offer quite so odd as, for example, the intra-haemocoelic insemination of *Cimicoidea* and

related bugs? There are, of course, abundant examples of ingenious adaptation for life in the soil and doubtless many routes to subaerial phytophagy do actually lie through soil-dwelling forms. But where such a path seems apparent the evidence is often somewhat equivocal. In the case of *Sminthurus viridis*, for example, derivation from the commoner litter habitat of other *Sminthurus* species is likely, but we note also the existence of the 'primitive' relative *Allacma fusca* which is associated with rotting wood and fungi. Similarly two rather unexpected pests of vines, *Lethrus*\* and *Vesperus* (Balachowsky & Męsnil, 1935), seem to have more connection with soil than rotting wood, but on surveying slightly more distant relatives this case too becomes more doubtful.

In a less dismissive approach to the competing claims of soil and litter a stand can be taken on the already mentioned weaker version of our thesis; that is, on the claim that, like dead trees, soil and litter forces subdivision and inbreeding on its inhabitants. Certainly a great deal of what has been said about necessities and adaptive responses of insects in dead trees applies to soil insects as well, and the evolutionary potential of these can be equally contrasted to that of the insects in more panmixial habitats on plants. It has to be insisted that neither in tree trunks nor in patchily distributed resources in the soil do we expect specially high rates of evolution *unless* some local inbreeding really occurs; if the resource, whatever its location, is used up in one generation and all offspring have to disperse and mix, then the species is certainly worse off than is, say, a coccid or a spider mite which is capable of local differentiation by drift through the perennation of its colonies and its restricted mobility. [Coccids have, in fact, very high rates of evolution at least for some traits (Nur, 1977); for tetranychid breeding structure see McEnroe (1969)]. Apart from soil insects this caution applies with force, as already mentioned, to a lot of dead-wood flies and beetles which have annual or longer life cycles. In being a more continuous habitat one might well expect soil and litter to enforce even less long-range dispersal than dead trees do; and the total loss of flying wings in many soil and litter insects of permanent habitats tends to confirm that this is so (see, e.g., den Boer, 1970). But unfortunately apart from the vague portent of such flightlessness we have little factual information about dispersal in environments presumed to be stable and uniform, either soil or any other. In the realm of theory too the problem remains little explored but models already developed make it clear that we cannot assume that existence of stable ongoing resource will imply minimal dispersal (Hamilton & May, 1977\*).

Rather as in the field of sociobiology the factor of relatedness has been added to others previously adduced in order to improve our understanding of, for example, evolution of social insects (e.g. Hamilton, 1972; West-Eberhard, 1975; Trivers & Hare, 1976), so the present considerations of breeding structure must be considered additions to a continuously improving, general picture of insect evolution. I see no conflict between the present emphasis on dead trees and Ghilarov's (1956) emphasis on soil as mediating transition to drier habitats, or with Hinton's (1977) deduction that conditions of alternate dryness and flooding were important in the stem of endopterygote evolution. Dead trees in a showery climate, indeed, almost idealise the concepts of these writers — a wick through which insects can evaporate to the air.

\*Recently Comins has found it possible to extend the models cited in such a way that less dispersal probabilities can be given for some of the classical breeding structures of population genetics (Comins, Hamilton and May, in prep.), so far, however, this development is more relevant to expected inbreeding and other properties for the 'stepping stone'-type distributions of dead tree insects than it is for the more purely 'viscous'-type distributions here supposed typical of soil insects.



## WATER

Equally, trees fallen into water could encourage transition to fully aquatic life. The idea that insects as a whole originate in aquatic habitats is now almost abandoned; consequently even the modern palaeopteran orders have to be regarded as secondarily aquatic. I am not aware that these orders show any hint of a significant connection with dead trees or even with litter. (The terrestrial litter-dwelling larva of *Megalagrion oahuensis* in forest litter is obviously a re-transference to land.) Inability to flex the wings flat over the abdomen in these orders also strongly contraindicates any connection with bark (contrast the habitat and presence of this ability in Liposcelidae and Phylloxeridae with lack of it in related families); but then of course the arborescent plants had no substantial kind of bark at the time these groups originated.

For most of the rest of the numerous invasions of water by insects, a route through dead trees seems more possible but is not strongly indicated against routes through other kinds of wet litter. This particularly is true for the Diptera, and, as already indicated for Ceratopogonidae, there may be some good cases for transition from water into rotting trees on land rather than the reverse. However, a phyletic closeness of 'wood' and 'water' is also indicated by a surprising number of families and these are mostly at the 'primitive' end of the dipteran range; examples are Tipulidae, Chironomidae, Ceratopogonidae, Syrphidae, Stratiomyiidae, Tabanidae, Dolichopodidae.

In Trichoptera the species with exceptional terrestrial larvae are not considered primitive. The larva of *Xiphocentron*, for example, lives on the outside of damp rotting trunks and that of *Enoicycla* lives in moss and litter. But both occur in woodland and so faintly suggest that tree trunks partly in water could have provided a bridge — to land in these cases, but also, perhaps, in an ancestor, to water. According to Ross (1967) the most primitive genera of Trichoptera are strongly convergent to a habitat of 'cool, moderately rapid small streams running through shaded woodland'. Trunks partly in water are particularly common in such places. With regard to the Megaloptera, such trunks at about the water level do in fact provide the headquarters of *Chauliodes* (Needham & Betten, 1901) a genus which well connects terrestrial subcortical raphidians with the more fully aquatic genera such as *Corydalis* and *Sialis*. Notwithstanding some claims (e.g. for Coleoptera, instancing *Corydalis*, Bradley, 1947) there seems no need to suppose that any major group of insects, excepting possibly Diptera, has arisen via an ancestral aquatic larva. However, the distribution of fresh water itself often imposes a pattern of small demes so that the evolutionary characteristics of this habitat may not be so very different from those of dead trees. In fact, ponds and streams (Riley, 1920; Parshley, 1922; Southwood, 1962) are indeed, like dead trees and grass tussocks (Luff, 1964), sites where wing polymorphism is common. And, corresponding to taxa of dead trees, aquatic taxa evidently also survive long, are often dubbed 'primitive' and at the same time manifest many very original adaptations: mention may be made here of labial masks of Odonata, subimagos of Ephemeroptera, the cases and feeding devices of Trichoptera. Paedogenesis has been achieved by Chironomidae. Male haploidy has not evolved in aquatic insects but Plecoptera seem to approach it, and outside the Arthropoda its only other full attainment is in an aquatic phylum, Rotifera.

## POLLEN

Examples of primitivity in this habitat are few but quite striking. Here examples from three groups must suffice. Adult Micropterygidae feed on pollen but their larvae apparently on



bryophytes – perhaps also on rotting materials. This family is regarded as the basal branch of the Lepidoptera, and by some as perhaps sister group to the Trichoptera. Three primitive genera of the Curculionoidea, *Cimberis* (Nemonychidae), *Allocorynus* (Oxycorynidae) and *Bruchela* (Anthribidae) breed, respectively, in male cones of *Pinus*, of *Zamia* and in the seed-capsules of *Reseda*. The last beetle and site merit mention here because the carpels of *Reseda* show an unusual primitive gymnospermous character – they are not closed. Such ‘primitive’ genera connected with sporangia of ‘primitive’ plants convey an obvious suggestion. However, they are but three genera in an immense group; and even with attention confined to these families plus the others that are primitive for the superfamily (e.g., Aglyceridae and Brentidae), habitats in the dead-tree complex are far more abundantly represented than are attachments to microspores. A transference of diet from mycelium to fungal spores and thence to pollen is not difficult to imagine; Crowson (1974) suggests such a transference in *Micrambe* (Cryptophagidae). A close parallel to the situation of these curculionoids exists in the symphytan Hymenoptera; *Xyela* can be compared to *Cimberis*, Siricidae to Brentidae, and the sawflies to the weevils. Malyshev (1969) thought that *Xyela* might betray the diet of the mecopteran-hymenopteran ancestor, i.e., microspores scattered on forest litter. In view of what has been said above a stem through mycetophagy with early branches to spore and pollen feeding seems at least equally likely. Wood, litter, moss, pollen and even water all cluster near to the faint phantom of the earliest hymenopteran. It is possible that, in the near future, uncovering the lives of the Meropeidae may slightly brighten this dim scene.

Pollen feeding is sometimes far from primitive. In connection with the unexpected pollen-feeding and other evolutionary novelties of heliconiine butterflies (Gilbert, 1972; this symposium) it is relevant to note that these insects seem unusually capable of creating a structure of small demes through their own social behaviour (Turner, 1971). In this they show a parallel tendency to polygynous eusocial insects (Hamilton, 1972) and to mammals (Wilson *et al.*, 1975). Such animals can speed their evolution without need for the kind of *forced* deme structure which, as this essay supposes, dead-tree cavities have provided to so many juvenescent groups of insects.

#### APPENDIX: Insect wing polymorphisms from live and dead trees

Table 10.2 lists genera containing species which are both colonial inhabitants of cavities in dead trees and polymorphic for wings in the adults. For this table wing polymorphism is interpreted broadly as any natural co-occurrence among adults of some individuals capable of flight and others incapable: hence sexual flight dimorphisms are potentially included (e.g. *Xyleborus*, with flying wings always vestigial in the male and always functional in the female). The kind of correlation between flight and sex is indicated in the last column; a key to symbols used in this column is given below the table. In some cases a category has been assigned on the basis of pooled information regarding several species.

The last column of Table 10.2 shows that slightly more frequently than not the wing-sex correlation leans towards males being more commonly flightless than females. Flightlessness of males when females can fly is strongly indicative of inbreeding (Hamilton, 1967); likewise an opposite condition, flightless females combined with flying males tends to indicate outbreeding, although this second implication is less definite than the first. Very small winged males of such flightless-female species, as of coccids, *Dusmetia*, some sciarids etc.,

Table 10.2. Flight-polymorphic insects living inside dead trees

ORDER	Habitat			Food	Wing-sex Association
	Sub-group <sup>†</sup>	Under dead bark	In sound wood	In rotted wood	
ZORAPTERA					
	*Zorotypus	x		x	Fungi? Mites? —
PSOCOPTERA					
	*Embiopsocus	x			Yeasts, etc —
	Psoquilla	x			Yeasts, etc
THYSANOPTERA					
	Megathrips	x			Spores —
	Cryptothrips	x			Spores —
	*Hoplothrips, etc.	x			Fungi —
HEMIPTERA					
	Aradidae	x			Fungi —?
	Henicocephalidae	x			Arthropods +
	*Xylocoris, etc.	x			Arthropods —
COLEOPTERA					
	Micromalthus			x	Wood, fungi? x
	*Ptinella	x			Fungi —
	Pteryx	x			? —
	Astatopteryx	x			? ?
	*Xyleborus		x		Fungi — —
DIPTERA					
	*Heteropeza	x		x	Fungi x
	*Pezomyia	x		x	Fungi +
	Micropteromyia	?		?	Probably fungi —
	Platosciara	?		?	Probably fungi +
	Coenosia	?		?	Probably fungi +
	*Pnyxia	x			Probably fungi +
	Sciara semialata	?		?	Probably fungi — —
HYMENOPTERA <sup>†</sup>					
	Sycosoter	x			Beetle larvae +
	Theocolax		x		Beetle larvae +
	*Cephalonomia	x		x	Beetle larvae +
ACARINA					
	*Pygmephorus <sup>††</sup>	x		x	Fungi —

\*Groups personally observed by the author.

<sup>†</sup>Species where either (a) female lays eggs by ovipositor from outside of bark, or (b) male is both large and winged, are considered incapable of continuous colonial life inside dead trees and are excluded from the list. Notable exclusions by this rule are in Hymenoptera, for example *Eupelmella* by (a), and Thynnidae by (b). In Diptera *Chonocephalus* has relatively large males and phoretic copulation like Thynnidae and sometimes breeds under bark; absolute smallness of males and their agility argues for inclusion of this genus suggesting that continuous colonies would be possible, but the fact that rotting fruit is more typical habitat than bark argues for exclusion.

<sup>††</sup>This genus of mites shows phoretomorphs analogous to the winged morphs of subcortical insects (see Hamilton, *in press*; Moser & Cross, 1975).

— All males flightless, all females capable of flight. — One or both sexes polymorphic such that males are more often flightless than females. ? Data on wing-sex correlation is lacking or inconclusive, or, in other columns that the main site of breeding is uncertain. + One or both sexes polymorphic such that females are more often flightless than males. x Species with thelytokous paedogenesis; outbreeding status unclear.

Table 10.3. Insect groups living externally on trees and showing some species with male winged and female flightless

ORDER Subgroup <sup>†</sup>	Habitat			
	Bark		Leaves	Food
	Sometimes inside	Outside		
DICTYOPTERA				
Blattaria	x	x		Omnivorous
Perlamantinae	?	x		Arthropods
EMBIOPTERA		x		Lichens, etc
PSOCOPTERA		x		
HEMIPTERA				
Coccoidea		x	x	Sap
Microphysidae	?	x		Arthropods
COLLEOPTERA				
Ptinidae	?	x		Lichens, etc
LEPIDOPTERA				
Psychidae		x	x	Leaves
Lymantridae			x	Leaves
Geometridae			x	Leaves

probably normally mate in their natal colony even though they might and sometimes do fly to enter other colonies. In insects as a whole such condition, with the female sex the more flightless, is far more common than the reverse. This fact underlines the hint of inbred colonies given by the correlations indicated in Table 10.2. In flightless-female species the sex ratio is usually about normal (1:1) whereas in flightless-male species (including all those known from dead trees) the sex ratio is female-biased. This also has an understandable connection with inbreeding (Hamilton, 1967). If flightless-female species are relative outbreeders and flightless-male species relative inbreeders, the suggestion from Table 10.2 that subcortical habitats of dead trees force on some types of inhabitants a more than usual amount of inbreeding is further reinforced by noting that on the *exterior* of bark (and on the exterior of the living tree as a whole) we find a majority of all the flightless-female conditions that are known. Flightless-male conditions, on the contrary, are here far more rare and, when they occur, occur along with some kind of special cover that could confine the colony (e.g. *Archipsocus*, with colonies living under self-made webs – it must be admitted, however, that the contrast between polymorphism in *Archipsocus* and in *Reuterella* or bark-dwelling Embioptera, which also live in webs, remains puzzling). Table 10.3 summarises the well-known flightless-female groups that are known on trees. Trees are so favoured by flightless-female species because trees are particularly exposed to wind and this allows for passive dispersal, usually by young larvae (Ghilarov, 1966).

To avoid over-encumbering the reference list of this paper, supporting references for the statements of Tables 10.2 and 10.3 are not given: full bibliography will be included in a future publication. Groups for which the author has personal experience and data are marked with an asterisk.

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